

INTERIM REPORT

(31 December 2012)

For project **task (#2)** entitled:

Occupancy models for monitoring songbird species on the Kaibab National Forest.

USFS-NAU Agreement # 09-CR-11030700-019 (Mod #3; *NAU Goshawk*)

Submitted to:

The Kaibab National Forest

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Recommended citation:

Williamson, M. A. and B. G. Dickson. 2012. Occupancy models for monitoring songbird species on the Kaibab National Forest. Interim Report to the Kaibab National Forest. Lab of Landscape Ecology and Conservation Biology, Northern Arizona University, Flagstaff, AZ. 8pp.

Project overview

As part of an existing cost reimbursable agreement between the Kaibab National Forest (KNF) and the Lab of Landscape Ecology and Conservation Biology at Northern Arizona University, this interim report encompasses the integration of digital forest structure data layers and ‘local-scale’ field measurements into updated spatially explicit estimates of occupancy probability for songbirds on the KNF. This task (#2) also compliments features of, and is an addendum to, the occupancy work presented in Dickson et al. (2011).

We derived forest-scale statistical models of habitat occupancy for three potential Management Indicator Species (Grace’s Warbler (*Dendroica graciae*), Ruby-crowned Kinglet (*Regulus calendula*), and Western Bluebird (*Sialia mexicana*)). These species are being evaluated for their ability to respond to future forest management actions as part of a revision of the Kaibab National Forest Land Management Plan. These previous analyses (described in detail in Dickson et al. 2011) demonstrated the utility of different ‘landscape-scale’ forest structural metrics, derived using remotely sensed imagery, to generate predictions of avifaunal occupancy across the entire Kaibab National Forest, and for species that could be sensitive to changes in forest structure, including changes due to mechanical thinning treatments or prescribed fire. For the previous analyses, we limited our analysis to landscape-scale environmental variables that were: a) obtainable using the Landsat Thematic Mapper (TM) satellite platform (or derived from those products) and b) likely to change as a function of forest management activities. Here we update, extend, and refine the original analyses by incorporating several additional variables collected in the field by the Rocky Mountain Bird Observatory (RMBO). These data were collected in conjunction with the avian surveys used to build the previous landscape-scale models.

Methods

A comprehensive description of avian survey methods, derivation of landscape-scale environmental variables, and the approach for assigning values for a variable to each transect appears in Dickson et al. (2011). For this report, spatially explicit models (and maps) of occupancy are not provided because it is not possible to derive these models when local-scale predictors of occupancy are not available in a continuous fashion (i.e., as raster grids) across the study area. Based on the results presented below, the spatially explicit occupancy models (and associated parameter estimates) presented in Dickson et al. (2011) are strong and remain current.

DERIVATION OF ENVIRONMENTAL VARIABLES

We used the same set of derived environmental variables from the previous analyses to update our spatially explicit models of occupancy (see Dickson et al. 2011). Habitat measurements were collected based on the RMBO point-transect methodology (Hanni et al. 2009). We incorporated field-collected (i.e., ‘local scale’) data that were: a) deemed to be accurately and consistently collected by field technicians (Pavlacky and Blakesley, pers. comm.) and b) predicted to be relevant to either the detection process, occupancy process, or both. Snags,

structural stage, and shrub height were averaged across points to generate a mean value for each transect across years. In contrast, we used the maximum estimate of grass cover to reduce the impact of inter-annual variability on this variable. Prior to implementing our occupancy models, we standardized and rescaled values for all continuous environmental variables, with the exception of snags, vegetation structure, and shrub height, to a mean of zero and unit variance (Neter et al. 1996). Continuous variables with Pearson correlation coefficients > 0.70 and relatively low interpretability were omitted from analysis.

ESTIMATING OCCUPANCY USING LOCAL- AND LANDSCAPE-SCALE VARIABLES

We applied the single-season occupancy framework (MacKenzie et al. 2006) used in our previous analyses to generate estimates of occupancy that again leveraged songbird survey data collected by the RMBO from 2006-2009 on the Kaibab National Forest. We defined occupancy (ψ) as the expected probability that a given site (i.e., transect) was occupied by a species during the period of analysis and detection probability (p) as the probability of detecting the species at a site if it was present during a count in that period (also defines the ‘detection process,’ MacKenzie et al. 2006). We derived estimates for ψ and p separately based on ‘full’ models that simultaneously included the most parsimonious model for the other parameters (Dickson et al. 2009). We used Akaike’s Information Criterion (AIC; Burnham & Anderson 2002) to identify the ‘best’ model(s) among a candidate set of nested models that each represented *a priori*-determined combinations of the local- and landscape-scale variables defined in Table 1 and described in Dickson et al. (2011). We also included null models of occupancy and detection probability (denoted by ‘dot’ models) within each candidate set to evaluate the performance (and fit) of the best models (Anderson 2008). We considered candidate models with AIC difference (ΔAIC) values < 4.0 as those that best approximated the data and used these models to calculate model-averaged regression coefficients ($\hat{\beta}$) and unconditional standard errors (Burnham & Anderson 2002). The relative strength of each predictor variable was evaluated using a Z statistic. We considered a variable with a Z value $> |2.0|$ to be a reasonably ‘strong’ predictor of occupancy, and used the sign of this value to interpret the direction of the relationship. Models that failed to converge or produced invalid parameter estimates were not considered in a candidate set of models used for inference. We conducted all analyses using the single season occupancy estimation routine in program PRESENCE (v2.2; Hines 2006).

Results

Similar to the results described in Dickson et al. (2011), models relating both local- and landscape-scale variables to occupancy performed better than null models of occupancy (ΔAIC always > 17.2 ; Table 1). Model results for Grace’s Warbler and Ruby-crowned Kinglet again showed a much stronger relationship with environmental variables than Western Bluebird and exhibited less model selection uncertainty. In general, inclusion of local-scale variables, particularly into models of the detection process, strengthened the ability of environmental variables to predict occupancy. In all cases, the inclusion of local-scale variables resulted in an increased number of strong predictors; however, with the exception of grass cover (and snags

for Ruby-crowned Kinglet), these strong predictors were always landscape-scale forest structure variables, i.e., derived from Landsat TM imagery (Dickson et al. 2011).

Previous model selection results (based only on landscape-scale variables) for Grace's Warbler indicated basal area and both low and intermediate canopy cover to be strong predictors of Grace's Warbler occupancy (Z-scores of 3.42, 2.06, and 2.01, respectively). Including local-scale variables in models of Grace's Warbler occupancy increased the strength of basal area as a predictor (Z-score of 3.90, Table 2) and also resulted in the standard deviation of both basal area and tree density being identified as strong predictors (Z-scores of 2.16 and -2.37, respectively; Table 2). The local-scale measure of grass cover was also a strong predictor (Z-score of 2.13; Table 2) and likely served as a more parsimonious expression of the relationship previously seen between canopy cover and Grace's Warbler occupancy. Previous models of occupancy (again based only on Landsat TM-derived variables) for Ruby-crowned Kinglet indicated basal area and the ponderosa pine vegetation type were the only strong predictors (Z-scores of 2.73 and -2.67, respectively). Inclusion of local-scale variables resulted in the standard deviation of tree density ($Z = 2.28$), low canopy cover ($Z = -3.28$), ponderosa pine vegetation type ($Z = -3.10$; Table 2), average number of snags ($Z = 2.39$), and grass cover ($Z = 5.81$) all identified as strong predictors of kinglet occupancy.

Predicting Western Bluebird occupancy remained challenging with considerable model- and variable-selection uncertainty as evidenced by the number of models with $\Delta AIC < 4.00$, and the few strong predictors in both iterations of the analyses. Presence of the ponderosa pine vegetation type was the only strong predictor in models of bluebird occupancy relying solely on Landsat TM-derived variables ($Z = 2.52$). Including local-scale variables identified presence of the mixed conifer vegetation type to be a strong negative predictor of occupancy ($Z = -2.41$), a similar expression of an affinity for the ponderosa pine vegetation type. In addition, grass cover also served as a strong predictor of bluebird occupancy in the new model set ($Z = 2.23$).

Discussion

We extended our analysis of forest structure-based (derived using satellite imagery), management-relevant predictors of occupancy to include a number of local-scale variables hypothesized to be more biologically important to Grace's Warbler, Ruby-crowned Kinglet, and Western Bluebird. Our updated results indicated that data collected (or derived) at both local and landscape scales data play an important role in predicting occupancy for Grace's Warbler, Ruby-crowned Kinglet, and Western Bluebird. This result is consistent with other multi-scale studies of avifaunal-habitat relationships, where models of occupancy that incorporated both local- and landscape-scale environmental attributes consistently outperformed those incorporating attributes measured at a single scale, especially when predicting occupancy across larger areas (e.g., Bakermans & Rodewald 2006; Meyer & Thuiller 2006; McClure et al. 2012).

Inclusion of local-scale variables generally improved model performance (as evidenced by ΔAIC values) and increased the strength of many of the landscape-scale predictors of occupancy. With the exception of grass cover (and snags for Ruby-Crowned Kinglet), however, none of these variables were strong predictors of occupancy. The importance of grass cover for Grace's Warbler and Western Bluebird seems biologically plausible given these species have a preference for more open habitats (Stacier & Guzy 2002; Guinan et al. 2008). Interpreting this

result for Ruby-crowned Kinglet, however, is not as straightforward, given that all other predictor variables are more indicative of a more closed-canopy, mixed conifer forest where appreciable grass cover occurs in relatively small dispersed openings. The importance of variation in tree density may also point to forest settings where such variation is associated with the presence of grassy openings. Alternatively, this result may be a strong example of the challenges introduced by the multi-scale nature of habitat selection by songbirds, for example, due to mismatches in the scale(s) of 'true' habitat selection patterns, the scale and design of the avian survey effort, and the scale of environmental variable measurements. Indeed, that snags were not a strong predictor of occupancy by Western Bluebird, a cavity nester, may also indicate potential scale mismatches in the current data set.

Habitat selection (and thus occupancy) is an inherently hierarchical process in which birds are making decisions at several scales about which habitat features to occupy (Johnson 1980); a more biologically comprehensive habitat model for any bird species is likely to require investigation and measurement at multiple scales. Furthermore, arbitrary selection of the scale(s) for investigation may lead to conflicting or unclear results, especially if those investigations take place at a scalar "threshold" (Wiens 1989). This fact results in significant challenges when using multi-species survey data where associated habitat measurements are made at a scale determined by protocol and efficiency, rather than explicitly accounting for the biology of species of interest. This challenge is further exacerbated by the detection process, which is likely to occur at a scale that differs from the scales perceived by the species of interest.

Our results suggest that inclusion of local-scale environmental features in models of the detection process substantially improve overall model performance. This is likely a result of the fact that habitat measurements were taken within 50 m of the point and may better describe the habitat attributes in which the observation occurred, rather than the attributes the bird was using at the time of detection. Thus, we recommend that if the objective is a more 'biologically complete' model of occupancy, that surveys and habitat measurements be designed explicitly to address those scales known to be relevant to the species of interest. This approach should minimize the impacts of scale mismatches and permit a deeper understanding of the scales at which various habitat or environmental features are important. Alternatively, if the objective is a framework capable of predicting (or monitoring) the response of multiple species to forest management across the landscape, we recommend that local-scale habitat or environmental variables collected in the field be restricted to those likely to impact the detection process.

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Table 1. Results of occupancy model selection for Grace's Warbler, Ruby-crowned Kinglet, and Western Bluebird on the Kaibab National Forest (Arizona, USA), 2006-2009. Modeled effects (i.e., environmental variables) included basal area (BA), standard deviation of basal area (BA_SD), standard deviation of tree density (TPA_SD), variation in existing vegetation type (VarEVT), ponderosa pine vegetation type (VegPP), mixed-conifer vegetation type (VegMC) northeastern orientation (NE), shrub height (SHRB), Snags (SNAG), structural stage (STAGE), grass cover (GCVR), and percent canopy cover (CC35). Canopy cover is expressed as "1" for all values <35% (CC35). Squared term indicates the quadratic form of the variable (BA²). Null models are denoted by (.). Yearly (i.e., annual) differences in detection probability are denoted as (y). All models were conditioned on a single best model of detection probability (p), where p for Grace's Warbler, Ruby-crowned Kinglet, and Western Bluebird was a function of (y, BA, BA², BA_SD, TPA_SD, CC35, VegPP, VarEVT, NE, STAGE, SHRB), (y, BA, BA², BA_SD, TPA_SD, CC35, VegPP, VegMC, VarEVT, NE, SHRB, STAGE), and (y, BA, BA², TPA_SD, CC35, VegPP, VegMC, VarEVT, SHRB) respectively.

Model	K^1	AIC ²	ΔAIC^3	w_i^4
<i>Grace's Warbler</i>				
$\psi(BA, BA_SD, TPA_SD, SNAG, GCVR)$	20	2369.21	0.00	0.4935
$\psi(BA, BA_SD, TPA_SD, CC35, SNAG, GCVR)$	21	2371.02	1.81	0.1996
$\psi(BA, BA_SD, TPA_SD, CC35, VegMC, SNAG, GCVR)$	22	2372.02	2.81	0.1211
$\psi(BA, BA_SD, TPA_SD, GC)$	19	2372.44	3.23	0.0981
$\psi(.)$	15	2399.20	29.99	0.0000
<i>Ruby-crowned Kinglet</i>				
$\psi(TPA_SD, CC35, VegPP, SNAG)$	20	1392.07	0.00	0.3359
$\psi(TPA_SD, CC35, VegPP, SNAG, GCVR)$	21	1392.36	0.29	0.2905
$\psi(TPA_SD, CC35, VegPP, STAGE, SNAG, GCVR)$	22	1393.19	1.12	0.1919
$\psi(BA, TPA_SD, CC35, VegPP, STAGE, SNAG, GCVR)$	23	1394.96	2.89	0.0792
$\psi(.)$	16	1428.66	36.59	0.0000
<i>Western Bluebird</i>				
$\psi(BA_SD, VegPP, VegMC, SNAG, GCVR)$	18	2013.33	0.00	0.2301
$\psi(VegPP, VegMC, SNAG, GCVR)$	17	2013.33	0.00	0.2301
$\psi(BA_SD, VegPP, VegMC, VarEVT, SNAG, GCVR)$	19	2013.77	0.44	0.1846
$\psi(VegMC, SNAG, GCVR)$	16	2014.16	0.83	0.1519
$\psi(BA, BA_SD, VegPP, VegMC, VarEVT, SNAG, GCVR)$	20	2015.42	2.09	0.0809
$\psi(BA, BA_SD, VegPP, VegMC, VarEVT, STAGE, SNAG, GCVR)$	21	2016.60	3.27	0.0449
$\psi(VegMC, GCVR)$	15	2016.63	3.30	0.0442
$\psi(.)$	13	2030.57	17.24	0.0000

¹Total number of model parameters, including those used to estimate p

²Akaike's Information Criterion

³AIC difference value

⁴AIC model weight

Table 2. Model-averaged regression coefficients ($\tilde{\beta}$), unconditional standard errors (SE), and Z statistics (Z) for environmental variables included in the best model(s) (AIC<4.0; Table 1) of occupancy for Grace's Warbler, Ruby-crowned Kinglet, and Western Bluebird on the Kaibab National Forest (Arizona, USA), 2006-2009. Estimates of mean basal area, standard deviation of basal area, and standard deviation of tree density are based on standardization and rescaling of all variables prior to analysis, and conditioned on a single best model of detection probability (Table 1). Variables that were not estimated because they were absent from the best model set are denoted as "—".

Environmental variable	Grace's Warbler			Ruby-crowned Kinglet			Western Bluebird		
	$\tilde{\beta}$	SE	Z ¹	$\tilde{\beta}$	SE	Z ¹	$\tilde{\beta}$	SE	Z ¹
Basal area	2.69	0.69	3.90	0.03	0.09	0.32	0.03	0.09	0.36
Standard deviation of basal area	1.41	0.65	2.16	—	—	—	0.48	0.59	0.82
Standard deviation of tree density	-1.38	0.58	-2.37	0.62	0.27	2.28	—	—	—
Canopy Cover (≤35%)	-0.17	0.42	-0.40	-3.12	0.95	-3.28	—	—	—
Ponderosa pine vegetation type	—	—	—	-2.08	0.67	-3.10	1.09	0.99	1.11
Mixed-conifer vegetation type	-0.10	0.24	-0.42	—	—	—	-2.16	0.90	-2.41
Variation in vegetation type	—	—	—	—	—	—	-0.13	0.23	-0.59
Structural Stage	—	—	—	0.31	0.57	0.54	0.04	0.12	0.38
Snags	0.07	0.05	1.59	0.13	0.06	2.39	0.09	0.06	1.40
Grass Cover	0.76	0.36	2.13	0.32	0.06	5.81	0.85	0.38	2.23
Intercept	-0.49	0.48	-1.03	-0.87	2.41	-0.36	0.92	0.97	0.94

¹Computed as $\tilde{\beta} / SE$